

Taxonomy and Distribution of *Pyrola subaphylla* Maxim. (Pyroleae, Ericaceae)

KOHTAROH SHUTOH^{1,†,*}, SHINGO KANEKO² AND TAKAHIDE KUROSAWA²

¹Graduate School of Symbiotic Systems Science and Technology, Fukushima University, 1 Kanayagawa, Fukushima 960-1296, Japan; [†]Present Address: Faculty of Education, Niigata University, 2-8050, Ikarashi, Nishi-ku, Niigata, 950-2181, Japan. *kohshutoh@gmail.com (author for correspondence); ²Faculty of Symbiotic Systems Science, Fukushima University, 1 Kanayagawa, Fukushima 960-1296, Japan

Pyrola subaphylla (Pyroleae, Ericaceae), which generally produces reddish scapes and scale-like or extremely small leaves, has been treated as a variety or form of the closely related *P. japonica*, which generally has green scapes and fully developed leaves, owing to observations of individuals with intermediate morphology. Recently, these two taxa were shown to differ genetically, supporting recognition of *P. subaphylla* as a distinct species. We identified herbarium specimens as *P. subaphylla* when (1) at least three shoots were mounted on the same sheet, (2) leaf blades <3.0 cm in length were present on all mounted shoots, and (3) at least one flowering shoot either lacked ordinary leaves, which are distinguished from scale-like leaves with blade >1 cm long, or bore only a single ordinary leaf. A revised taxonomic treatment of the species is proposed. In Japan, *P. subaphylla* occurs in Hokkaidō, Honshū (Tōhoku and Chūbu district), and Shikoku, usually in coniferous forests at 0–1,500 m.

Key words: distribution, Ericaceae, Japan, Pyroleae, *Pyrola japonica*, *Pyrola subaphylla*, taxonomy

Pyrola japonica Klenze ex Alef. s. l. (Pyroleae, Ericaceae), a perennial herb in section *Ampliosepalae* series *Japonicae* (Liu *et al.* 2010), is distributed in Japan, Korea, and China (Hebei, Heilongjiang, Henan, Jilin, Liaoning, Nei Mongol, and Taiwan; Takahashi 1993, Qin & Stevens 2005). It is closely related to *P. elegantula* Andres and *P. decorata* Andres (Liu *et al.* 2010, 2014), which have narrowly oblong leaves with an acute apex and oblong or obovate-oblong leaves with white stripes along the veins of the adaxial leaf surface, respectively (Qin & Stevens 2005). *Pyrola japonica* is distinguished by its broadly ovate to elliptic leaves with an obtuse to rounded apex and lacks white stripes (or stripes are inconspicuous) on the veins of the adaxial leaf surface (Qin & Stevens 2005). For the past 100 years, *P. japonica* s. l. has been consistently treated as a single species. However, Shutoh *et al.* (2016) re-

ported that *P. japonica* s. l. in Japan includes at least seven chloroplast haplotypes (A–G) and exhibits variation in leaf size that is correlated with the haplotypes.

Haplotype G is distinguished from the other chloroplast haplotypes by more than two nucleotide substitutions in three non-coding plastid regions (*trnT-trnL* intergenic spacer, *rpl16* intron, and *ndhA* intron). Plants carrying haplotype G are characterized by reddish scapes and significantly smaller leaves (Shutoh *et al.* 2016). The haplotype and morphological traits are usually fixed within a population. Consistent congruence between haplotype and morphology has been interpreted as indicating that little gene flow occurs between populations harboring haplotype G and populations of the other haplotypes (Shutoh *et al.* 2016). In addition, when developing simple sequence repeat (SSR) markers, different allele sets

were detected between populations that were representative of haplotype G and the other most abundant haplotype, haplotype A (Shutoh *et al.* 2017). Therefore, in accordance not only with the biological species concept (Mayr 1969), but also with the evolutionary species concept (Wiley 1978) and the phylogenetic species concept (Cra-craft 1989), haplotype G can be justifiably treated as a species distinct from the other haplotypes of *Pyrola japonica*.

As already mentioned, haplotype G is characterized by reddish scapes and 0–3 (mean = 1.0) ordinary leaves <3.4 (mean = 2.2) cm long and <3.0 (mean = 1.8) cm wide, which are distinguished from scale-like leaves >1 cm long (Figs. 1 & 2; Shutoh *et al.* 2016). However, the number and size of the ordinary leaves vary greatly among the other haplotypes. From an analysis of herbarium specimens, haplotypes A through F that lack or bear only a few small ordinary leaves are difficult to distinguish from haplotype G because the color of the scapes tends to fade. Therefore, to distinguish haplotype G from other haplotypes, it is necessary to examine the morphology of multiple shoots per population.

Based on the few and small leaves, Shutoh *et al.* (2016) considered that haplotype G may correspond with the taxon *Pyrola japonica* var. *subaphylla* (Maxim.) Andres, which was initially described from specimens collected at three localities in Japan (Hokkaidō, Mt. Fuji, and Nagano Prefecture) and was characterized by a single leaf per shoot (Maximowicz 1867). Although Maximowicz (1867) described *P. subaphylla* as a distinct species, it has also been treated as an intra-specific taxon of other Asian species of *Pyrola* by subsequent authors. Makino (1913) treated it as *P. rotundifolia* L. var. *incarnata* DC. f. *subaphylla* (Maxim.) Makino [as “var. *incarnata* (Fisch.) DC. forma *subaphylla* (Maxim.) Makino”], referring to it as “an accidental form” in the habitat of var. *incarnata*. Given that the number of flowers and leaf shape of *P. subaphylla* differ from those of *P. incarnata*, no other authors have adopted Makino’s (1913) treatment. Instead, Andres (1914) considered *P. subaphylla* to be more closely related to *P. japonica* Klenze ex Alef. and

treated it as *P. japonica* var. *subaphylla* (Maxim.) Andres. Subsequent authors have either followed Andres’s (1914) or treated it as a form of *P. japonica* (Ohwi 1953).

In this study, we analyzed previously published data (Shutoh *et al.* 2016) to determine morphological characteristics that define populations putatively fixed for haplotype G. We used morphological characteristics to distinguish the taxa on herbarium specimens of *Pyrola japonica* s. l. We also examined the type specimens of *P. subaphylla* to determine if they were morphologically consistent with the haplotype. The type specimens of *P. japonica* f. *rosiflora* H. Hara and other subaphyllous taxa, *P. incarnata* var. *subaphylla* and *P. denticulata*, were also examined. The taxonomic treatment and geographic distribution of *P. japonica* s. l. is discussed, and an identification key is provided. We define *P. japonica* s. s. as exhibiting haplotypes A–F, while *P. japonica* s. l. is defined as comprising haplotypes A–G, as in Shutoh *et al.* (2016, 2017).

Materials and Methods

Discrimination of haplotype G

Using raw leaf area data from Shutoh *et al.* (2016), in which shoots in populations putatively fixed for haplotypes A, D, and G were measured, we calculated the probabilities (P_A , P_D , P_F , and P_G) that three randomly selected flowering shoots of haplotypes A, D, F, and G, respectively, would each exclusively have leaves <3.0-cm-long. The probabilities P_A , P_D , P_F , and P_G were estimated as 0.0024, 0.0089, 0.2441, and 0.9474, respectively (Table 1), suggesting that haplotypes G and F can be distinguished from haplotypes A and D when at least three randomly selected shoots bear leaves <3.0-cm-long. We also calculated the proportion (P_L) of flowering shoots with two or more leaves to distinguish haplotype G from haplotype F, because all flowering shoots from haplotype F bore two or more ordinary leaves (Shutoh *et al.* 2016). The P_L of haplotype G was 0.063 (Table 2), suggesting that haplotype G can be distinguished from haplotype F by having at least one flowering

TABLE 1. Probability that all leaves of three randomly selected flowering shoots from *P. japonica* s. s. (haplotypes A, D, and F) and *P. subaphylla* (haplotype G) bear leaves <3.0 cm in length.

Taxon (haplotype)		N_{fs}	$N_{<3.0\text{ cm}}$	$P_{<3.0\text{ cm}}$	Probability
<i>P. japonica</i> s. s.	(A)	67	9	0.134	0.0024
	(D)	106	22	0.208	0.0089
	(F)	8	5	0.625	0.2441
<i>P. subaphylla</i>	(G)	224	220	0.982	0.9474

N_{fs} , number of flowering shoots examined; $N_{<3.0\text{ cm}}$, number of flowering shoots with leaves <3.0 cm long; $P_{<3.0\text{ cm}}$, proportion of flowering shoots with leaves <3.0 cm long. N_{fs} and $N_{<3.0\text{ cm}}$ are raw data from populations with single haplotypes in Shutoh *et al.* (2016).

TABLE 2. Proportion of flowering shoots with two or more leaves on *Pyrola japonica* s. s. (haplotype F) and *P. subaphylla* (haplotype G).

Taxon (haplotype)		N_{fs}	$N_{L>1}$	$P_{L>1}$
<i>P. japonica</i> s. s.	(F)	8	8	1.000
<i>P. subaphylla</i>	(G)	224	14	0.063

N_{fs} , number of flowering shoots examined; $N_{L>1}$, number of flowering shoots with >1 leaves; $P_{L>1}$, proportion of flowering shoots with >1 leaves. N_{fs} and $N_{L>1}$ are raw data from populations with single haplotypes in Shutoh *et al.* (2016).

shoot with 0–1 ordinary leaves. We did not consider the morphology of haplotypes B, C, and E, owing to the scarcity of samples and their co-occurrence within two populations (Shutoh *et al.* 2016).

Examination and identification of herbarium specimens

To determine the morphology and distribution of haplotype G, we examined more than 300 herbarium specimens of *Pyrola japonica* s. l. in K, E, SAPS, IUM, TUS, YAMA, FKSE, TNS, TI, KYO, OSA, MAK, KANA, and MBK, including type specimens of *P. subaphylla* and the related taxa *P. japonica* f. *rosiflora* H. Hara and *P. incarnata* var. *subaphylla* Satomi. Based on the raw data from Shutoh *et al.* (2016), we identified herbarium specimens as haplotype G when (1) at least three shoots were mounted on a single sheet, (2) each mounted shoot bore a leaf with a blade <3.0 cm long (distinguishing them from haplotypes A and D), and (3) at least one flowering shoot either lacked ordinary leaves or had only a single ordinary leaf (distinguishing them from haplotype F). We also used photographs and label descriptions of scape color to aid in identification if those were indicated. Specimens with fewer than three shoots were included when the

haplotype had been determined by Shutoh *et al.* (2016). In contrast, specimens with leaves ≥ 3.0 -cm long were identified as *P. japonica* s. s. Based on our identifications, we created distribution maps for *P. subaphylla* and *P. japonica* s. s., as well as scatter plots of the elevation and latitude based label data from specimens of both the *P. subaphylla* and *P. japonica* s. s.

The frequency by which we were able to identify the species (*Pyrola subaphylla* or *P. japonica* s. s.) from herbarium specimens was also calculated (P_1), using specimens deposited in TUS and FKSE. The probability was calculated by dividing the number of identifiable sheets by the number of sheets examined. Specimens that we collected were excluded from the analysis to avoid overestimating P_1 , because those specimens generally included at least three mounted shoots.

Results and Discussion

Identity of *P. subaphylla* and related taxa and nomenclature of haplotype G

The identity of two type specimens of *Pyrola subaphylla* was confirmed using our identification method. For one syntype (Maximowicz s. n., K463688) comprising eight flowering shoots, five

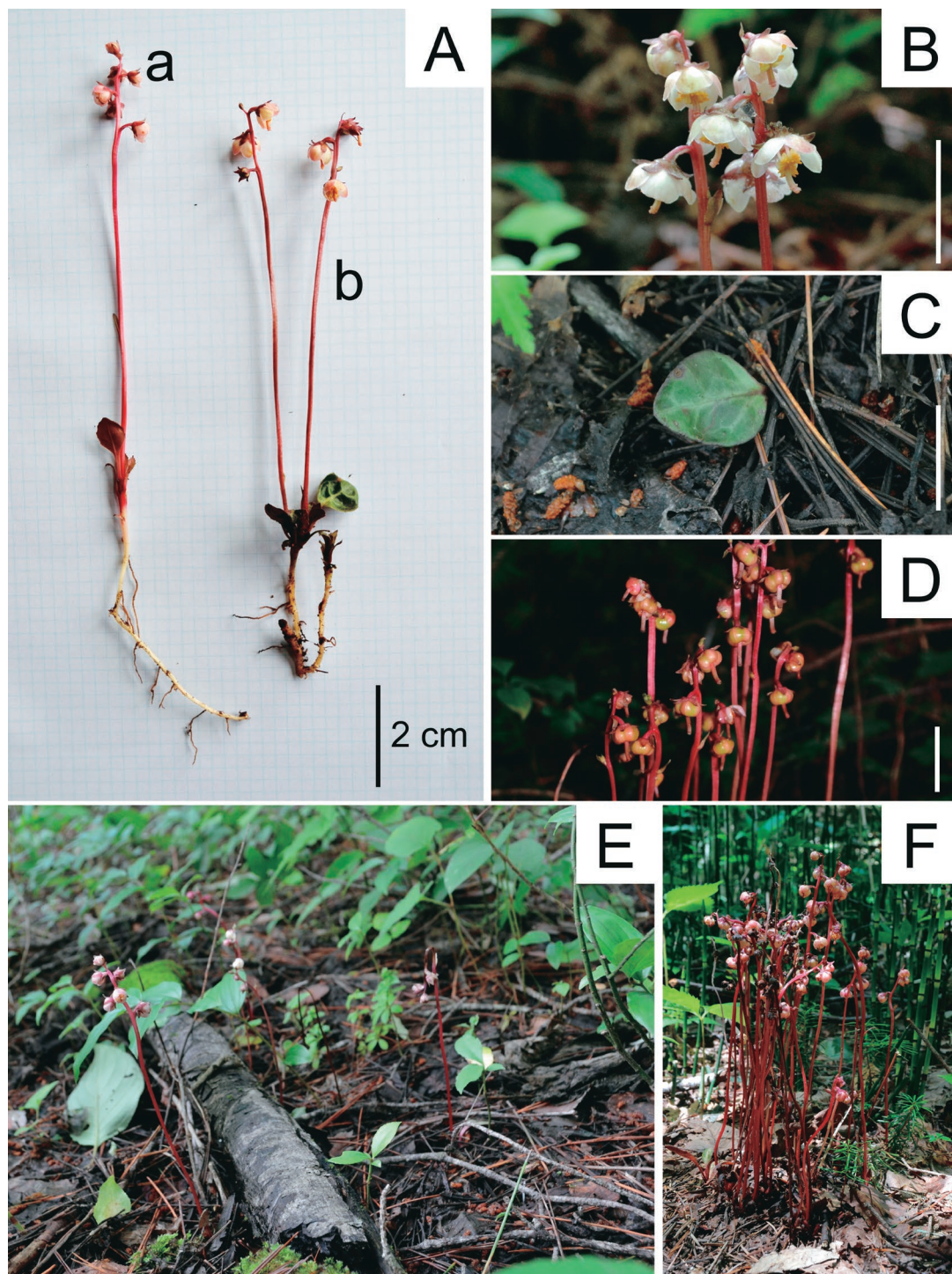


FIG. 1. *Pyrola subaphylla* Maxim. A, habit (a, shoot with scale-like leaves; b, individual plant with small ordinary leaf); B, flowers; C, ordinary leaf; D, fruits; E, habitat; F, large individual. Photographs taken at Mt. Bandai-san, Fukushima Prefecture, Japan, on 10 July 2016 (A, B, C, and E); Mt. Neko-dake, Nagano Prefecture, Japan, on 28 August 2014 (D); and Sapporo-shi, Hokkaidō Prefecture, Japan, on 20 July 2012 (F). Scale bars represent 2 cm.

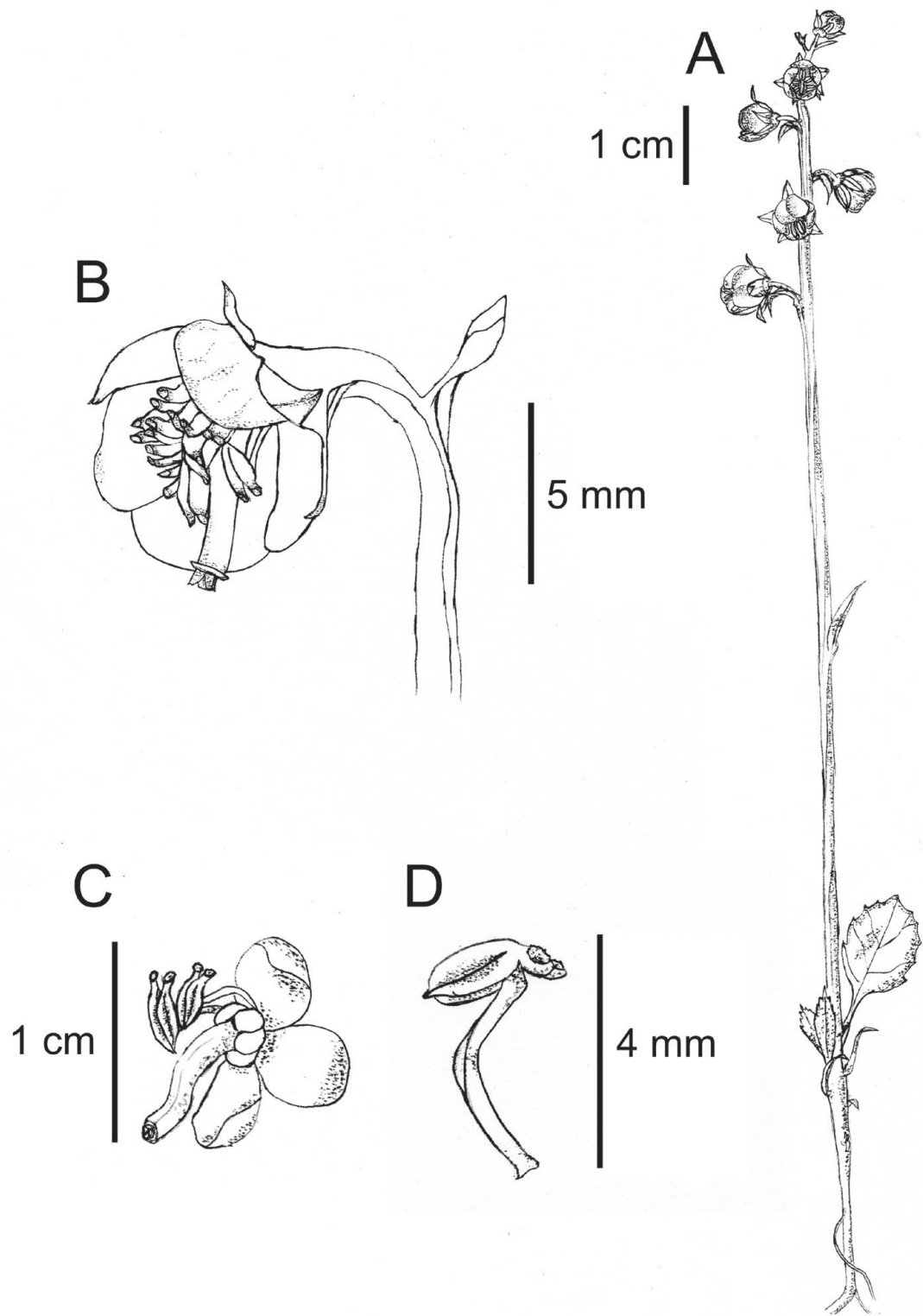


FIG. 2. *Pyrola subaphylla* Maxim. A, habit; B, flower; C, ovary; D, stamen. Drawn by Masako Yamaguchi (A, C, and D) and Kohtaroh Shutoh (B).

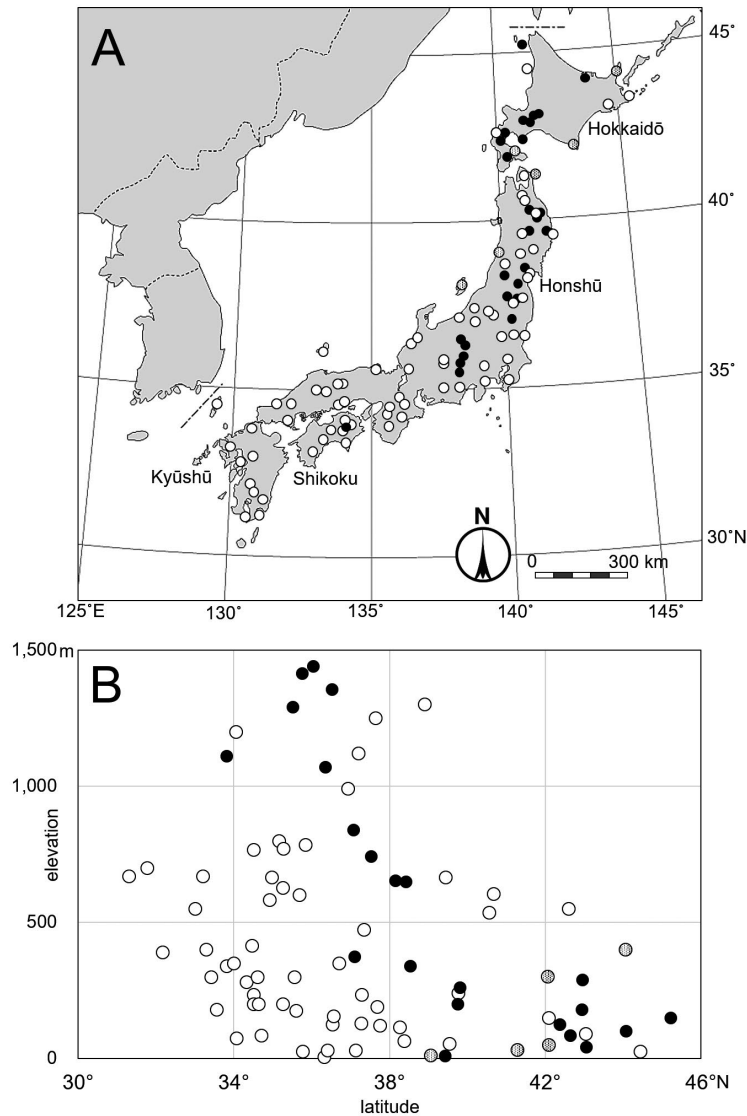


FIG. 3. Distributions of *Pyrola subaphylla* (haplotype G in shutoh *et al.* 2016) and *P. japonica* s. s. (haplotypes A–F) in Japan. A, distribution map; B, scatter plot showing elevation and latitude (using only specimens with elevation data recorded). Specimens examined are listed in Appendix 1. Black circles, *P. subaphylla*; white circles, *P. japonica* s. s.; stippled circles, sympatric *P. subaphylla* and *P. japonica* s. s.

TABLE 3. Number of identifiable and unidentifiable specimens in TUS and FKSE and probability of identifiable specimens of *P. subaphylla*.

	Identifiable specimens		Unidentifiable specimens		P_1
	$P. subaphylla$	$P. japonica$ s. s.			
	$S_N \geq 3$ $B_L < 3.0$ cm	$B_L \geq 3.0$ cm	$S_N \geq 3, L_N > 1$, $B_L < 3.0$ cm	$S_N < 3$, $B_L < 3.0$ cm	
TUS	18	192	0	15	0.93
FKSE	4	46	1	4	0.91
Total	22	238	1	19	0.93

B_L , blade length; L_N , leaf number; P_1 , probability of identifying *P. japonica* s. l. specimens; S_N , number of mounted shoots.

Key to the species of *Pyrola* in Japan

The following key from Takahashi (1993), has been modified to account for both *Pyrola japonica* s. s. and *P. subaphylla*.

- 1a. Flowers bilaterally symmetrical; anthers not surrounding pistil; style exserted, curved 2
- 1b. Flowers radially symmetrical; anthers surrounding pistil; style included or barely exserted, straight or slightly curved 7
- 2a. Leaves reniform-orbicular, basal margins overlapping; winter buds completely naked; young scapes nodding, slender; sepals orbiculate, apex obtuse *P. renifolia* Maxim.
- 2b. Leaves depressed orbicular to elliptic, basal margins not overlapping; winter buds completely enveloped in scales; young scapes erect, stout; sepals triangular to elliptic, apex acute to acuminate 3
- 3a. Scales often leaf-like, costae distinct; winter buds incompletely enveloped in scales; leaves often with white stripes along veins 4
- 3b. Outer scales white membranous, costae indistinct; winter buds completely enveloped in scales; leaves without white stripes along veins 5
- 4a. Leaves ordinary or sometimes scale-like, ordinary leaves (blade >1 cm long) usually several; blade of ordinary leaves often more than 3 cm long; young scape green or reddish *P. japonica* Klenze ex Alef. s. s.
- 4b. Most leaves scale-like or considerably reduced, ordinary leaves usually less than two; blade usually less than 3 cm long; scape reddish or sometimes green in fruit *P. subaphylla* Maxim.
- 5a. Bracts lanceolate to widely lanceolate; sepals longer than wide 6
- 5b. Bracts widely linear; sepals shorter than or as long as wide *P. alpina* Andres
- 6a. Leaves wider than long; anthers creamy white *P. nephrophylla* Andres
- 6b. Leaves longer than wide; anthers dark purple *P. incarnata* (DC.) Freyn
- 7a. Anthers to 2 mm long; style 2.5–4 mm long, barely exserted; sepals ovate, more than 2 mm long; bracts more than 1 mm wide *P. fauriana* Andres
- 7b. Anthers about 1 mm long; style 1–2 mm long, included; sepals ovate-triangular, less than 2 mm long; bracts less than 1 mm wide *P. minor* L.

shoots bore either a small (<2.5 cm long) ordinary leaf or a few scale-like (≤0.5 cm long) leaves; three shoots lacked ordinary leaves. For another syntype (*Maximowicz s. n.*, GH61386 photo) comprising three flowering shoots, one of the shoots lacked ordinary leaves, one had a small (about 2 cm long) ordinary leaf, and one had two small (<2 cm long) ordinary leaves. Other characteristics of haplotype G, including the scale-like leaves and petals, also correspond to the original description of *P. subaphylla* (Maximowicz 1867). Thus, the correct name for haplotype G is *Pyrola subaphylla* Maxim. when the haplotype is treated as a distinct species.

Pyrola incarnata var. *subaphylla* Satomi, which has reduced scale-like leaves, was previously described as an aphyllous variant of *P. incarnata* (Satomi 1955). The holotype of the variety (*M. Takahashi s. n.*, KANA17259), which was collected from Mt. Asama (Nagano Prefecture), has a shoot with three flowers and no ordinary leaves. However, the floral morphology, especially flower number, suggests that it more likely represents *P. japonica* s. l. (1–11 flowers, mean = 4),

rather than *P. incarnata* (4–19 flowers, mean = 10). It was difficult to determine whether the type specimen of *P. incarnata* var. *subaphylla* was identical with *P. subaphylla*, because the type specimen has only a single shoot. However, an additional specimen collected near the type location (about 5 km from the top of Mt. Asama), identified as *P. incarnata* var. *subaphylla* by Satomi (*N. Satomi* 7838, KANA19971), had 11 flowering shoots, of which eight had no leaves and the remaining three each bore a small ordinary leaf. Based on our criteria, we identified this specimen as *Pyrola subaphylla*, but it remains unclear whether *P. incarnata* var. *subaphylla* is also haplotype G.

Pyrola denticulata Koidz. was originally described from Mt. Komagatake (Hokkaidō) as having leaves 1.3–2.2 cm wide and 1.4–2.8 cm long with serrate margins (Koidzumi 1916). Hara (1936) noted that *P. denticulata* is part of a series that connects the subaphyllous form with *P. japonica* s. l. and treated it as a synonym of *P. japonica* var. *subaphylla*. Koidzumi (1916) did not cite a type specimen when he described *P. den-*

ticulata, but a specimen (Collector unknown, *s. n.*, August 7, 1878, TI) collected from the type locality and with a label identifying it as *P. japonica* Klenze var. *denticulata* (Koidzumi) may represent original material that was available to the author. The specimen consists of a single shoot with three leaves <3.0 cm in length. It may therefore be synonymous with *P. subaphylla*, but further study is needed.

Nakai (1939) identified a specimen from Mt. Hayachine, Iwate Prefecture (S. Hattori *s. n.*, TI) as *Pyrola asarifolia* Michx., based on its large leaves and large flowers with reddish petals. Hara (1948) later correctly identified the specimen as *P. japonica s. l.* and described it as a new form, *f. rosiflora* H. Hara. The holotype is a single shoot that bears 10 large ordinary leaves and a scape of unknown color. We believe the specimen represents *P. japonica s. s.*, but it is unclear which haplotype (A–F) the specimen represents. Based on its reddish color, the specimen could possibly be morphologically intermediate between *P. japonica s. s.* and *P. subaphylla*.

Morphology and distribution of *P. subaphylla*

The description of *Pyrola subaphylla* is revised based on 50 specimens collected from Japan (Appendix 1). Although the morphology of the pollen and some reproductive organs of *P. subaphylla* and *P. japonica s. s.* were previously reported as identical and only slightly different, respectively (Takahashi 1986, Tonkova 2013), the specimens analyzed in those previous studies should be re-examined in light of the data presented here, especially because specimens with fewer than three shoots are sometimes difficult to identify.

In Japan, we found that *Pyrola subaphylla* has a disjunct distribution (Fig. 3a). Most of the populations occur in Hokkaidō and both northern and central Honshū, but an isolated population was recently discovered in Shikoku (Shutoh *et al.* 2014). In addition, *P. subaphylla* occurs at high latitudes and altitudes, whereas *P. japonica s. s.* is distributed more widely (Fig. 3b). Although *P. subaphylla* has also been occasionally reported from the Russian Far East, northeastern China,

and Korea (Komarov & Klobukova-Alissova 1932, Kitagawa 1939, 1979, Chou & Zhou 1990, Lee 1996), the specimens that we were able to identify as *P. subaphylla* were restricted to Japan. Therefore, further studies are needed to confirm the identity of *Pyrola* from Russia, China, and Korea.

Both Hatusima & Sato (1994) and Kagoshima Prefecture (2003) reported *Pyrola subaphylla* to occur on Yakushima, Kyūshū, Japan. However, a photograph in Hatusima & Sato (1994) shows shoots with green scapes and extremely small leaves. Our preliminary molecular analysis indicated that samples from Yakushima that exhibit such morphologies are haplotype A, which is typical of *P. japonica s. s.* (Shutoh unpublished data). Therefore, we do not treat the Yakushima plants as *P. subaphylla*.

Identification problems

Among the 280 herbarium specimens of *Pyrola japonica s. l.* from TUS (*n* = 225) and FKSE (*n* = 55), 22 specimens were identified as *P. subaphylla* and 238 as *P. japonica s. s.*; 20 specimens were unidentifiable (Table 3). About 93% of the specimens could be identified using our identification method. Although the proportion of unidentifiable specimens was relatively low, authentic specimens, such as the type specimens of *P. incarnata* var. *subaphylla* and *P. denticulata*, could not be identified.

Specimens that we regarded as *Pyrola subaphylla* might have included individuals with haplotypes B, C, E, or F because variation in leaf morphology and scape color is incompletely understood (Shutoh *et al.* 2016). Those haplotypes, however, are apparently relatively rare and local in Japan, and such haplotypes are likely to have larger leaves than plants with haplotype G (Shutoh *et al.* 2016). Therefore, we expect that the frequency of haplotypes B, C, E, and F in specimens we identified as *P. subaphylla* should be low and that their inclusion would hardly affect our descriptions or the morphology and distribution.

Shutoh *et al.* (2016) reported haplotype A as probably corresponding to *Pyrola japonica s. s.*

and suggested that the remaining haplotypes (B–F), which are currently difficult to discriminate from haplotype A using only herbarium specimens may represent *P. japonica* s. s., an intraspecific taxon of it, or a cryptic species (Shutoh *et al.* 2016). Although *P. japonica* s. s. is paraphyletic in the parsimony network of Shutoh *et al.* (2016), we treat it as a species in our revised taxonomy. It is at least likely that haplotype D should be treated as a species according to the results based on SSR markers (Shutoh unpublished data). To determine the taxonomic status of plants with haplotypes B–F, it will be necessary to sample additional populations and haplotypes. Additional DNA analyses with more comprehensive sampling will be needed.

Taxonomic treatment

Pyrola subaphylla Maxim. —Figs. 1 & 2

Pyrola subaphylla Maxim. in Bull. Acad. Imp. Sci. Saint-Petersbourg sér. 3 11: 433 (1867) and Mélanges Biol. Bull. Acad. Imp. Sci. Saint-Petersbourg 6: 206 (1867); Miquel, Prolus. Fl. Jap.: 382 (1867); Maximowicz in Bull. Acad. Imp. Sci. Saint-Petersbourg 18: 54 (1873); Franchet & Savatier, Enum. Pl. Jap. 1: 295 (1875); Makino in Bot. Mag. (Tokyo) 11: (451) (1897); Boissieu in Bull. Herb. Boissier 5: 923 (1897); Matsumura, Index Pl. Jap. 2(2): 450 (1912). —*Pyrola rotundifolia* L. var. *incarnata* (Fisch.) DC. f. *subaphylla* (Maxim.) Makino in Bot. Mag. (Tokyo) 27: 24 (1913); Makino & Nemoto, Fl. Jap.: 433 (1925); Makino & Nemoto, Fl. Jap. rev. ed.: 860 (1931). —*Pyrola japonica* Klenze ex Alef. var. *subaphylla* (Maxim.) Andres in Oesterr. Bot. Z. 64: 245 (1914); Andres in Bull. Jard. Bot. Buitenzorg. ser. 3 14(1): 4 (1936); Hara in Bot. Mag. (Tokyo) 50: 490 (1936), as “(Maximowicz) Hara”; Hara in Bot. Mag. (Tokyo) 52: 625 (1938); Hara, Enum. Sperm. Jap. 1: 5 (1949); Honda, Nom. Pl. Jap.: 255 (1939); Kitamura & Murata, Col. Ill. Herb. Pl. Jap. I, Symp.: 238 (1957); Yamazaki in Satake *et al.*, Wild Flow. Jap. Herb. Pl. 3: 5 (1981); Takahashi in Iwatsuki *et al.*, Fl. Jap. 3a: 67 (1993). —*Pyrola japonica* Klenze ex Alef. f. *subaphylla* (Maxim.) Ohwi [Fl. Jap.: 875 (1953), *nom. nud.*] in Bull. Natl. Sci. Mus. Tokyo 33: 81 (1953); Honda, Nom. Pl. Jap.: 185 (1957); Honda, Nom. Pl. Jap. ed. emend.: 185 (1963); Ohwi, Fl. Jap. rev. ed.: 1011 (1965); Ohwi, Fl. Jap. ed. Engl.: 691 (1965); Sugimoto, Keys Herb. Pl. Jap. I, Dicot.: 406 (1965); Ohwi, Fl. Jap. new ed. rev. enl.: 1011

(1975); Ohwi & Kitagawa, New Fl. Jap.: 1138 (1983). —Syntype: Japan. Hokkaidō, Hakodate, Siginope (“ins. Yeso, circa Sigi-nope”), Maximowicz s. n., 19 July 1861 (K463688! & GH61386 photo!); Mt. Fuji (“Fudzi”); Nagano Prefecture (“prov. Senano”).

Pyrola incarnata (DC.) Fisch. ex Freyn var. *japonica* auct. non (Klenze ex Alef.) Koidz., Fl. Symb. Orient.-Asiat. 74 (1930); Koidzumi, *ibid.*, p. p.; Nemoto, Fl. Jap. suppl.: 549 (1936), p. p.

Description. *Herbs*, evergreen, perennial; aboveground parts (excluding ordinary leaves) deep or pale reddish when young; deep reddish, pale reddish, or pale green in fruit; rhizomatous, forming rosettes. *Leaves* scale-like or ordinary, sometimes indistinguishable. Ordinary leaves (blade >1 cm long) 0–2(–5); petiole 0.5–4 cm long; blade broadly elliptic or obovate, 1–4 cm long, 0.5–3 cm wide. Scale-like leaves (blade <1 cm long) several, lanceolate, 3–12 mm long, 1–5 mm wide. *Scape* deep or pale reddish when young; deep reddish, pale reddish, or pale green in fruit; 5–26 cm long. *Flowers* 1–8 per scape, bilaterally symmetrical, drooping; petals 5, ovate, pale pink or white, 5–7 mm long, 4–6 mm wide; sepals 5, deep or pale reddish, widely lanceolate to narrowly ovate, 3–6 mm long, apex acute; style exerted or scarcely exerted, gently curved, 4.5–7.6 mm long after flowering; stigma about 1 mm wide; stamens 10; anthers white, about 2 mm long, with two yellow pores; pedicel curved, 2–10 mm long; bract on pedicel, resembling scale leaves 0–3 on scape below inflorescences, lanceolate, acuminate, deep or pale reddish when young, deep reddish, pale reddish, or pale green in fruit, 4–12 mm long, 1–3 mm wide. *Fruit* a capsule, 5-valved, dehiscent, 3.5–5 mm long, 4–7 mm wide; seeds about 1 mm long, winged. *Flowering* June to August. *Fruiting* August to October.

Japanese name. Hitotsuba-ichiyakusō (Makino 1897).

Distribution. Hokkaidō, Honshū (Tōhoku and Chūbu district), and Shikoku, Japan (Fig. 3a). Usually in dense shade in coniferous forests. Elevation 0–1,500 m (Fig. 3b).

Note. Andres (1910) has sometimes been cited in the taxonomic treatment of *P. subaphylla* (Andres 1914, Hara 1948, Chou & Zhou 1990), but

the cited page number, 22, is erroneous; Andres' (1910) paper is actually on pp. 50–54. *P. subaphylla* is not mentioned in the paper.

We thank the associate editor and two anonymous reviewers for constructive comments, M. Briggs and S. Dawson (K), A. Ebihara (TNS), S. Kawakami and K. Sawa (YAMA), M. Maki and K. Yonekura (TUS), J. Murata (TI), H. Nagamasu (KYO), C. Pendry and M. F. Watson (E), Y. Sasaki (IUM), H. Takahashi (SAPS), M. Yokogawa (OSA), N. Murakami (MAK), N. Shintani (MBK), and K. Ueda (KANA) for facilitating examination of herbarium specimens, O. Yano for facilitating fieldwork, and M. Yamaguchi for preparing the illustrations. This work was supported by the Research Project of Fukushima University for Regeneration of Harmonies between Human Activity and Nature in Bandai-Asahi National Park, the Nichirei Corporation, and a Grant-in-Aid from the Japan Society for the Promotion of Science Research Fellowship [No. 15J12267].

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Received November 18, 2016; accepted May 1, 2017

APPENDIX 1. Specimens examined.

Pyrola subaphylla Maxim.

- JAPAN. Hokkaidō:** Rishiri Isl. (*M. Hotta* 2015, 28 August 1959, OSA; *S. Okamoto* 1762, 20 August 1956, KYO); Shari-gun, Shari-ō (*H. Takahashi* 262, 7 July 1978, TUS42079); Suttu-gun, Kuromatsunai-chō (*H. Yamaji* 4757, 20 July 1997, TUS330986); Tokoro-gun, Saromachō (*H. Takahashi* 241, 6 July 1978, TUS42094; *H. Takahashi* 240, 6 July 1978, SAPS21047); Mt. Komagatake (*H. Takahashi* 272, 12 July 1978, TUS42067); Kayabegun, Shikabe-chō (*M. Hara* 5720, 20 July 1980, SAPS20956); Samani-gun, Samani-chō (*H. Yamaji* 518, 10 August 1996, TUS375272); Sorachi-gun, Kurisawachō (*Y. Gouda* 731, 22 July 1990, KYO); Ebetsu-shi, Nopporo (*N. Satomi* 24144, 18 July 1966, MAK236493; *M. Hara* 3143, 27 July 1987, SAPS21008; *K. Miyabe* s. n., 4 July 1914, SAPS21016); Sapporo-shi, Jouzankei (*H. Nakamura* s. n., 27 July 1994, MAK331942); Sapporo-shi, Chōu-ku (*Y. Yamashita* 662, 10 June 2015, FKSE86848); Muroran-shi, Mizumoto-chō (*M. Hara* 5724a, 23 August 1978, SAPS20952); Futami-gun, Yakumo-chō (*H. Morita* s. n., 17 September 1983, KYO); Hiyama-gun, Assabu-chō (*M. Hara* 5724b, 27 July 1978, SAPS20953); Hakodate (*Maximowicz* s. n., 19 July 1861, K463688).
- Honshū, Tōhoku Distr., Aomori Pref.:** Shimokita-gun, Higashidori-mura (*H. Takahashi* 316 & 320, 18 July 1978, TUS42049–42050 & 42051; *K. Yoshioka* & *K. Sugawara* s. n., 30 August 1964, TUS6568). **Iwate Pref.:** Moriokashi (*K. Shutoh et al.* 1957, 4 July 2012, FKSE90727); Kunoh-gun, Yamagata-mura (*M. Kikuchi* 231, 25 July 1952, IUM); Iwate-gun, Kuzumaki-machi (*M. Kikuchi* s. n., 8 July 1959, IUM); Ninohe-gun, Jōbōji-machi (*M. Kikuchi* s. n., 20 July 1958, IUM); Shimohei-gun, Iwaizumi-chō (*M. Takahashi* s. n., 12 August 1979, TI); Shimohei-gun, Yamada-chō (*T. Fukuda et al.* 25, 7 July 2000, TUS252682). **Yamagata Pref.:** Akumi-gun, Yuzamachi (*H. Ōhashi* s. n., 18 July 1960, TUS6567); Nishimurayama-gun, Nishikawa-chō (*K. Shutoh et al.* 1255 & 1256, 29 June 2014, FKSE86102 & 86103). **Miyagi Pref.:** Kami-gun, Kami-machi (*K. Shōji et al.* 5817, 14 July 1997, TUS428120); Shibata-gun, Kawasaki-chō, Mt. Zao (*A. Kimura* & *S. Sugaya* s. n., 6 July 1950, TUS6586). **Fukushima Pref.:** Fukushima-shi (*Y. Hayashi* s. n., 7 August 1984, TUS100870); Yama-gun, Inawashiro-machi (*K. Shutoh* 514, 31 July 2013, FKSE82295); Yama-gun, Kitashiobara-mura (*K. Shutoh* & *H. Takahashi* 1263, 2 August 2012, FKSE86110); Shirakawa-shi (*S. Suzuki* s. n., 28 June 1933, TUS280624).
- Chūbu Distr., Niigata Pref.:** Sado Isl. (*Y. Tsukamoto* s. n., July 1940, KYO). **Nagano Pref.:** Kitasaku-gun, Karuizawa-machi, Oiwake (*N. Satomi* 7838, 30 July 1956, KANA19971); Kitasaku-gun, Karuizawa-machi (*K. Shutoh* & *M. Matsui* 1261, 15 August 2012, FKSE86108; *J. Haginiwa* 20830, 20831 & 20841, 8 August 1984, TNS970830, 970831 & 970841); Ueda-shi (*K. Shutoh* & *A. Aoyagi* 1162, 28 August 2014, FKSE85572); Mt. Yatsugatake (*H. Kanai* 2309, 11 July 1950, TI); Shimoina-gun, Oshika-mura (*K. Asano* & *H. Asano* s. n., 3 June 2009, MAK387683); Ina-shi (*S. Fujii* 16320, 14 September 2014, KYO).
- Shikoku, Tokushima Pref.:** Naga-gun, Naga-machi (*K. Shutoh et al.* 167, 14 June 2013, FKSE69490). **Kōchi Pref.:** Kami-gun, Monobe-son (*T. Yamawaki* M72-108, 5 August 1972, MBK38933).
- P. japonica* Klenze ex Alef. sensu stricto**
- JAPAN. Hokkaidō:** Shari-gun, Shari-chō (*H. Takahashi* 261, 7 July 1978, TUS42080); Nemuro-shi (*T. Sasaki* 361, 20 August 1988, KYO); Kawakami-gun, Shibeche-chō (*K. Takita* 690, 9 August 1981, KYO); Samani-gun, Samani-chō (*H. Yamaji* 10061, 18 August 2007, TUS390777; *K. Yonekura* & *H. Akutagawa* 95677-b, 29 July 1995, TUS308834); Tokomae-gun, Haboro-chō, Yagisiri Isl. (*E. Miki* 1148, 21 July 1980, OSA35720); Shimamaki-gun, Mt. Karibayama (*H. Hoshi et al.* 1143, 3 August 1984, TUS108954); Mt. Komagatake (*H. Takahashi* 274, 12 July 1978, TUS42069).
- Honshū, Tōhoku Distr., Aomori Pref.:** Shimokita-gun, Higashidori-mura (*H. Takahashi* 308, 18 July 1978, TUS42048); Mutsu-shi, Mt. Osore-zan (*T. Kyōgoku* & *Y. Hayashi* s. n., 26 June 1959, TUS6562); Aomori-shi (*K. Yonekura* 5384, 27 July 2004, TUS308134); Towada-shi (*K. Yonekura et al.* 12862, 25 July 2005, TUS324968). **Iwate Pref.:** Esashi-gun, Hada-mura (*H. Iwabuchi* 2680, 13 June 1933, TUS51549); Miyako-shi (*K. Yonekura* 20026, 11 July 2013, TUS427016); Iwate-gun, Takizawa-

mura (*M. S. Takahashi* 28, 11 July 1973, TUS40179); Mt. Hayachine (*S. Hattori s. n.*, 10 August 1927, TI, type of *Pyrola japonica* Klenze ex Alef. f. *rosiflora* H.Hara). **Akita Pref.:** Ogachi-gun, Mt. Torage (*The staff of the Bot. Gard. s. n.*, 23 July 1970, TUS18040); Mt. Mahiru (*K. Shutoh et al.* 1871, 30 July 2015, FKSE89252). **Yamagata Pref.:** Akumi-gun, Yuza-machi (*H. Ōhashi s. n.*, 18 July 1960, TUS6566); Mt. Gassan (*C. Suzuki s. n.*, 11 August 1938, TUS355610). **Miyagi Pref.:** Sendai-shi (*K. Yonekura* 615, 4 July 1992, TUS168956); Kurokawa-gun, Taiwa-chō (*T. Naito & K. Hara* 77768, 29 July 1977, TUS428901). **Fukushima Pref.:** Fukushima-shi (*K. Shutoh & M. Yamaguchi* 1259, 27 July 2012, FKSE86106; *K. Shutoh & S. Sato* 1260, 11 July 2012, FKSE86107); Minamiaidzu-gun, Minamiaidzu-machi (*S. Kato et al.* 396, 4 August 2015, FKSE87450); Minamiaidzu-gun, Tadami-machi (*K. Shutoh et al.* 493, 8 June 2013, FKSE82274); Futaba-gun, Naraha-machi (*K. Yonekura* 6581, 10 October 2000, TUS255654).

Chūbu Distr., Niigata Pref.: Sado Isl. (*H. Marui s. n.*, 16 October 2008, OSA239378); Kariwa-gun, Oguni-machi (*S. Iwano* 18316, 2 October 1982, TUS416417); Minamiuonuma-gun, Yuzawa-machi, Mt. Takatsukura-yama (*T. Naito* 88006, 16 July 1988, TUS411644); Joetsu-shi (*K. Shutoh & T. Kurosawa* 2119, 23 September 2012, FKSE92441). **Ishikawa Pref.:** Kanazawa-shi (*K. Shutoh & K. Miyake* 93, 12 May 2013, FKSE69174); Kaga-shi (*T. Takeuchi* 301, 16 June 1992, TUS211446). **Nagano Pref.:** Kiso-gun, Ōkuwa-mura (*T. Sugawara* 1061606, 16 June 2001, TUS305901); Kiso-gun, Kiso-machi (*K. Yonekura & M. Hakozaki* 15981, 18 July 2008, TUS379660). **Shizuoka Pref.:** Haibara-gun, Kawabehon-chō, Mt. Sawaguchi (*F. Konta & T. Tsuno* 6090, 29 June 1967, TUS308839). **Aichi Pref.:** Kitashitara-gun, Toyone-mura, Mt. Chausu-yama (*T. Kato s. n.*, 10 July 1966, TUS18041).

Kantō Distr., Ibaraki Pref.: Katsuta-shi (*T. Naito & H. Okazaki* 801012, 10 October 1980, TUS429211). **Tochigi Pref.:** Utsunomiya-shi (*S. Suzuki s. n.*, 12 June 1963, TUS369024); Nasu-gun, Batou-machi, Mt. Torinokosan (*T. Nagayama* 214, 20 June 1983, TUS86597). **Chiba Pref.:** Mt. Kano-zan (*I. Hurusawa s. n.*, 20 March 1937, TUS18043); Ichikawa-shi (*M. Ohsawa* 1290, 5 August 1962, TUS18038). **Tōkyō Pref.:** Nishitama-gun, Hinohara-mura (*M. Ohba s. n.*, 9 October 1965, TUS18039). **Kanagawa Pref.:** Ashigarashimo-gun, Hakone-machi, Mt. Komagatake (*A. Murase s. n.*, 28 September 1952, TUS18044).

Kinki Distr., Mie Pref.: Nabari-shi (*K. Seto* 51505, 11 September 1999, OSA156476). **Shiga Pref.:** Ika-gun, Yogo-machi (*Y. Tateishi & T. Nemoto* 12390, 22 September 1987, TUS128195). **Kyōto Pref.:** Naka-gun, Mineyama-chō (*K. Seto* 42195, 23 July 1994, OSA99780); Sagara-gun, Mt. Jūbusen (*M. Hori s. n.*, 17 June 1951, OSA). Nara Pref.: Yoshino-gun, Kawakami-mura (*T. Umehara* 4779, 15 July 1992, OSA91330). **Ōsaka Pref.:** Yao-shi

(*T. Kodama* 9103, 16 June 1961, OSA); Kawachinagano-shi (*S. Fujii & T. Fujii* T-1081, 7 July 1988, OSA70757). **Wakayama Pref.:** Hidaka-gun, Ryūjin-mura, Mt. Gomadan (*T. Kodama* 11487, 25 July 1968, OSA8540).

Chūgoku Distr., Okayama Pref.: Tomota-gun, Kagaminochō (*S. Nemoto* 569, 16 July 2013, FKSE69095); Maniwa-shi (*K. Shutoh et al.* 2191, 24 October 2016, FKSE92517); Niimi-shi (*K. Shutoh et al.* 2193, 25 October 2016, FKSE92519); Okayama-shi, Mt. Tatsunokuchi-yama (*K. Shutoh et al.* 2190, 26 October 2016, FKSE92516); Kurashiki-shi, Mt. Hiruma-san (*R. Nishihara s. n.*, 22 June 1952, MBK40673). **Hiroshima Pref.:** Shobara-shi, Hiwa-chō (*K. Shutoh et al.* 265, 28 June 2013, FKSE81194); Hatsukaichi-shi (*N. Yonezawa et al. s. n.*, 17 August 2002, KYO). **Yamaguchi Pref.:** Kuga-gun, Shūtō-chō (*Y. Koga* 12324, 22 June 1996, KYO); Abugun, Abu-chō (*Y. Koga* 11950, 3 September 1995, KYO). **Shimane Pref.:** Oki-gun, Nishino-shima Isl. (*M. Okamoto* 1637, 19 November 1976, OSA150664).

Shikoku, Kagawa Pref.: Kagawa-gun, Shiono-machi (*M. Uchida s. n.*, 13 July 1969, TUS92843). **Ehime Pref.:** Iyomishima-shi (*T. Yamanaka* 529, 17 June 1939, TUS291963). **Tokushima Pref.:** Myozai-gun, Kamiyama-chō (*Y. Ibaragi* 2805006, 28 May 2001, TUS274201). **Kōchi Pref.:** Nagaoka-gun, Yoshino-mura (*T. Yamanaka* 8965, 18 July 1952, TUS382125); Hata-gun, Touwa-mura (*K. Takeuchi* FOK-611479, 27 May 2004, TUS320923); Takaoka-gun, Hidaka-mura (*M. Nomura* FOK-612875, 4 June 2004, MBK96736); Muroto-shi (*T. Matsumoto et al.* FOK-63083, 1 November 2003, MBK78008).

Kyūsyū, Fukuoka Pref.: Munakata-shi (*S. Watanabe* 10100, 10 May 1992, TUS235036). **Nagasaki Pref.:** Sasebo-shi (*K. Yonekura* 92740, 21 August 1992, TUS165512); Kamigata-gun, Mine-chō (*K. Yonekura* 8281, 6 May 2002, TUS278022); Minamitakaki-gun, Obama-chō, Mt. Fugen-dake (*A. Kimura s. n.*, 26 August 1925, TUS230263). **Miyazaki Pref.:** Ebino-shi (*K. Seto* 53062, 30 May 2000, OSA158500); Kitamorogata-gun, Mt. Higashi-dake (*M. Hutoh* 28948, 9 June 1968, OSA). **Kumamoto Pref.:** Kikuchi-shi (*S. Imae s. n.*, August 1959, TUS15711); Hitoyoshi-shi (*K. Yonekura* 18396, 27 June 2011, TUS395270). **Kagoshima Pref.:** Ibusuki-shi, Mt. Kaimon-dake (*S. Sugaya & K. Sōma s. n.*, 21 May 1960, TUS6580); Mt. Kirishima (*M. Hori* 939, 13 June 1953, OSA); Kimotsuki-gun, Uchinoura-chō (*K. Yonekura* 11091, 29 March 2004, TUS303067).

Unidentifiable specimens

JAPAN, Hokkaidō: Mt. Komagatake (*Collector unknown s. n.*, 7 August 1878, TI, type of *Pyrola incarnata* (DC.) Fisch. ex Freyn var. *subaphylla* (Satomi)).

Chūbu Distr., Nagano Pref.: Mt. Asama (*M. Takahashi s. n.*, 31 August 1952, KANA17259, type of *Pyrola denticulata* Koidz.).